

Observations on the radulae of *Physa acuta* (invasive) and *Bulinus tropicus* (indigenous) in relation to recolonisation

Observaciones sobre las rádulas de *Physa acuta* (especie invasora) y *Bulinus tropicus* (indígena) en relación con la recolonización

Therese D. BRACKENBURY*

Recibido el 16-II-1999. Aceptado el 22-VII-1999

ABSTRACT

In South Africa the invasive snail, *Physa acuta*, has repeatedly shown its ability to rapidly recolonise denuded habitats after flooding of the Umsindusi River. This was not the case for indigenous species, such as *Bulinus tropicus*, which were dependent on the return of marginal vegetation. Although previous investigations revealed that *P. acuta* possessed several attributes which contribute to its success, its feeding strategy in a denuded habitat was unknown. The present investigation found that the radula of *P. acuta* appeared to be adapted for harvesting/combing fine detritus or unicellular organisms (0.5 to 10 μm) while that of *B. tropicus* was adapted for rasping large sized food particles and filamentous algae ($\geq 20 \mu\text{m}$). The denuded substratum of the Umsindusi River was noted to be abundant in unicellular organisms while filamentous algae and detritus remained absent until the return of marginal vegetation. Therefore, it is possible that the radular structure and feeding mechanism of *P. acuta* was another contributing factor to its success as a coloniser.

RESUMEN

El caracol invasor *Physa acuta* ha mostrado repetidamente su capacidad para recolonizar hábitats arrasados por avenidas del río Umsindusi en Sudáfrica. Por el contrario, algunas especies autóctonas, como *Bulinus tropicus*, necesitaron una previa revegetación de las áreas devastadas. Aunque investigaciones precedentes señalaron que *P. acuta* posee varias características que favorecen este éxito en la recolonización, se desconce como influye en ella su estrategia trófica. Esta investigación pone de manifiesto que la rádula de *P. acuta* parece estar adaptada para ramonear sobre detritos finos y organismos unicelulares (0,5 a 10 μm), mientras que la de *B. tropicus* está adaptada a hacerlo sobre partículas alimenticias mayores y algas filamentosas ($\geq 20 \mu\text{m}$). Se halló que los organismos unicelulares pequeños son abundantes en el sustrato desnudo del río Umsindusi, mientras que éste carece de algas filamentosas y de partículas grandes hasta que se repuebla con vegetación. Por ello, la estructura de la rádula y la estrategia trófica de *P. acuta* se consideran factores que contribuyen a su éxito como colonizador.

KEY WORDS: radula, feeding mechanism, invasive, *Physa*, *Bulinus*.

PALABRAS CLAVE: rádula, estrategia trófica, invasiones, *Physa*, *Bulinus*.

* Biological Control Products Pty (Ltd), PO Box 1561, Pinetown 3600, South Africa.

INTRODUCTION

The invasion by aquatic pulmonates has been increasing in the rivers of southern Africa and a species of particular interest in South Africa is the North American aquatic snail, *Physa acuta* (Pulmonata: Physidae) (Draparnaud 1805) (BROWN, 1980). It has become established in many of South Africa's river systems (HAMILTON-ATTWELL, DE KOCK AND VAN EEDEN, 1970; DE KOCK, JOUBERT AND PRETORIUS, 1989). The snail has been recorded sporadically in the Umsindusi River (KwaZulu-Natal Province), but since 1986 the species has comprised between 66 - 94% of the local gastropod population (BRACKENBURY AND APPLETON, 1993). In 1987-88 the Umsindusi River was flooded on four occasions which extensively eroded the river channel removing all marginal vegetation and the associated fauna. However, *P. acuta* rapidly (30-90 days) recolonised the denuded bed on each occasion and in due time comprised between 80 - 100% of the gastropods present. The most common indigenous species, *Bulinus tropicus*, however, never exceeded 20% (BRACKENBURY, 1989). *Physa acuta* was observed to possess a number of attributes which appeared to contribute to its success as an invader

in the river; these included year-round breeding, high intrinsic rate of increase, broad thermal and high water current velocity tolerance, the absence of patent trematode infection (BRACKENBURY AND APPLETON, 1993, BROWN, 1994) and negligible predation (WILKEN AND APPLETON, 1991). *Bulinus tropicus* on the other hand did not possess these traits (BRACKENBURY, 1989; BRACKENBURY AND APPLETON 1991, 1993).

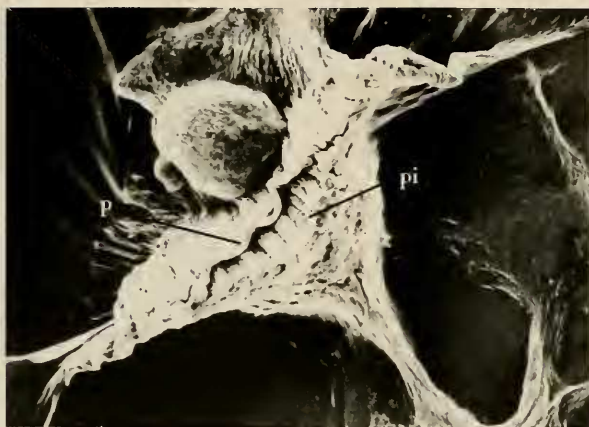
In a denuded river habitat, such as the Umsindusi River, snails attempting to recolonise an area would encounter, amongst others, difficulties in locating a readily available food supply. BRACKENBURY (1989) noted that newly established *P. acuta* populations fed off a rich diatom resource on the Umsindusi channel's substratum. Although this food supply was available in regions of low water current velocities, *B. tropicus*, only recolonised the area after marginal vegetation had returned. Plants not only provide protected holdfasts for the snails, but also an alternative food resource such as epiphytic algae, decaying macrophytes and fine detritus (PIMENTAL AND WHITE, 1959; CALOW, 1970; HUNTER, 1980; THOMAS, 1987; MADSEN, 1992). The question then arose:

(Right page) Figure 1. *Physa acuta* SEM. A: triangular jaw composed of a thin dorsal plate overlying numerous pillar-like structures; B: radular ribbon fully displayed showing symmetrical arrangement of teeth; C: nascent region with newly formed central teeth (single row) and lateral teeth (multiple rows on either side of central row); D: mid-region of ribbon supporting mature teeth; E: anterior region of ribbon which supports the old and worn teeth. Scale bars, A, C, E: 20 µm; B: 600 µm; D: 50 µm.

Abbreviations, a: anterior end; al: algae; c: central teeth; cr: central longitudinal row of teeth; e: cutting edges of jaw; l: lateral teeth; p: dorsal plate; pi: pillar-like structures; po: posterior end; r: region cleared of algae by the radula.

(Página derecha) Figura 1. *Physa acuta* MEB. A: mandíbula triangular compuesta por una fina placa dorsal que recubre numerosas estructuras en forma de pilar; B: rádula completa mostrando la disposición simétrica de los dientes; C: región de crecimiento con dientes centrales recién formados (una única línea) y dientes laterales (varias líneas a cada lado de la central); D: región media de la rádula, con dientes maduros; E: región anterior de la rádula con dientes viejos y deteriorados. Escalas, A, C, E: 20 µm; B: 600 µm; D: 50 µm.

Abreviaturas, a: borde anterior; al: algas; c: diente central; cr: fila central de dientes; e: borde cortante de la mandíbula; l: dientes laterales; p: placa dorsal; pi: estructuras en forma de pilar; po: borde posterior; r: áreas libres de algas por efecto de la rádula.



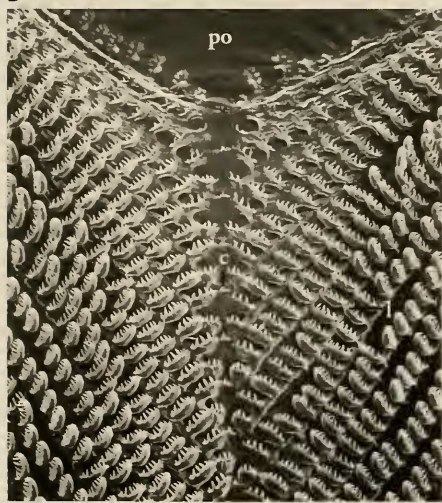
A



B



C



D



E

does the radula structure and rasping mechanism play an important role in contributing to the ability of *P. acuta* and *B. tropicus* to invade and colonise a barren habitat? The present study attempted to answer this question.

MATERIAL AND METHODS

Adult *P. acuta* and *B. tropicus*, with shell heights of 6.0 - 6.5 mm and 7.0 - 7.5 mm (median shell height) respectively, were collected from a pond in, Durban, South Africa (29° 49' S; 31° 01' E) and acclimatized in pond water in the laboratory for seven days. To study the structure of the radula ribbon, the buccal mass (n= 8) of both *P. acuta* and *B. tropicus* were removed from freshly killed snails and placed in a 5 ml solution of potassium hydroxide (\pm two pellets) and heated in a water bath (70°C) for two to five minutes. After the dissolution of the tissue the radular ribbon and attached jaw were isolated in 70% ethanol, sonicated and then mounted flat in a drop of ethanol on double sided tape. This was followed by gold-palladium coating (Polaron E5100 SEM Coating Unit) and viewed with a Hitachi F520 Scanning Electron Microscope (SEM). Live movement of the radula and odontophore was recorded using a VRC as snails (n= 10) travelled over algal coated Petri-dishes. To obtain the feeding track pattern of the two species the green unicellular alga, *Chlamydomonas* sp. (10 μ m)

was filtered onto micropore filter paper (pore size 0.45 μ m) coated paper was submersed in water over which individual snails (n= 10) (starved for two days) were allowed pass over. The papers were then removed, fixed in 3% glutaraldehyde in 0.05M phosphate buffer, critical point dried, carbon coated and viewed under a dissecting microscope and SEM. To observed the ability of the radula of each species to collect different sized food particles, microspheres (0.5 μ m), unicellular algae such as *Selenastrum capricorn* (6-7 μ m), *Bumilloeriopsis* sp. (10-12 μ m), and the filamentous alga (18-20 μ m) were collected separately on micropore filter paper as described above. Individual snails (n= 10) were allow to move and feed once over the paper which was then prepared as described above. Average particle densities before and after feeding were calculated from SEM micrographs.

RESULTS

Morphology: The roof of the buccal cavity of *P. acuta* (shell heights between 6.0 and 6.5 mm) supported a single, thin light brown, transverse triangular jaw (171 μ m x 37 μ m). SEM examination showed that the jaw was composed of a thin dorsal plate overlying numerous flat-ended pillar-like structures (Figure 1A). The odontophore supported a radular ribbon, a highly malleable mem-

(Right page) Figure 2. *Bulinus tropicus* SEM. A: the thick, darkly pigmented, sickle-shaped jaw with a narrow cutting edge; B: radular ribbon fully displayed showing symmetrical arrangement of teeth; C: nascent region with newly formed central teeth (single row) and lateral teeth (several rows either side of central row); D: newly formed and maturing marginal teeth which are located on the marginal edges of the ribbon; E: anterior region of the ribbon supporting extensively worn central and lateral teeth. Scale bars, A: 100 μ m; B: 350 μ m; C, D: 20 μ m; E: 30 μ m.

Abbreviations as in Figure 1.

(Página derecha) Figura 2. *Bulinus tropicus* MEB. A: mandíbula gruesa, oscura, en forma de hoz, con un borde cortante estrecho; B: rádula completa mostrando la disposición simétrica de los dientes; C: región de crecimiento, con dientes centrales recién formados (una única línea) y dientes laterales (varias líneas a cada lado de la central); D: dientes marginales recién formados, localizados en los bordes de la rádula; E: región anterior de la rádula, con dientes muy gastados. Escalas, A: 100 μ m; B: 350 μ m; C, D: 20 μ m; E: 30 μ m.

Abreviaturas como en la Figura 1.



A



B



C



D



E

brane to which numerous symmetrically arranged teeth were attached. The ribbon of *P. acuta* (shell height 6.7 mm - 7.5 mm), averaged 1733 μm long and 567 μm wide (Figure 1B), and covered an area of 5.3 mm^2 supporting approximately 5×10^4 teeth (9434 teeth/ mm^2). Longitudinal rows of teeth were identical only varying in size depending on maturity. The ribbon was symmetrically divided by the longitudinal row of centrals flanked on either side by up to 40 oblique rows of laterals. Morphologically distinct marginals were not evident. The centrals and marginals appeared delicate which implied that they were not used for cutting bulk foods. The small centrals were composed of a rectangular base ($9.9 \times 6.76 \mu\text{m}$) from which projected five cone-shaped cusps (length 1 to 3 μm) (Figure 1C). With the larger laterals the laterobasal and basal edges of the pyramidal stem were concave (Figure 1C). The apex of the stem expanded into the crown (width 12.76 μm) which had five large cusps (average length 5.83 μm) and six small interstitial cusps (average length 2.2 μm). The nascent region of the ribbon supported the newly formed teeth which were prolated and soft with finely point cusps while with each consecutive transverse row the teeth increased in size, and became more erect. Sequential rows of teeth showed slight, progressive and even wearing of the cusps (Figure 1D, E). Those of the centrals were reduced by 17% while the cusps and interstitial cusps of the laterals were reduced by 43% and 24.5% respectively (Figure 1E).

A description of the jaw and radula *B. tropicus* has been provided by STIGLINGH, VAN EEDEN AND RYKE (1962) and STIGLINGH AND VAN EEDEN (1976) and will not be expanded in this text. In the present study the jaw of *B. tropicus* (shell height between 7.0 and 7.5 mm) was similar to that observed by STIGLINGH, VAN EEDEN AND RYKE (1962) and STIGLINGH AND VAN EEDEN (1976), however, lateral jaws were not noted. Unlike *P. acuta* the jaw of *B. tropicus* was a dark pigmented, well developed, sickle-shaped dorsal plate with a

narrow cutting edge (Figure 2A) and the radular ribbon (averaging 1684 μm long and 670 μm wide) supported three morphologically distinct groups of teeth with an average density of 5882 teeth/ mm^2 (Figure 2B, C, D). The teeth morphologies observed in this study were similar to that described by STIGLINGH ET AL., (1962), however, the variation in shape of the central cusps was considered to be a consequence of wear and tear by the present author. In comparison to *P. acuta*, the teeth on the radula of *B. tropicus* were fewer in number, but larger in size and robustness, however, the extent of cusp wear was far greater in *B. tropicus*. In the mid-region of the ribbon the cusps had lost 78% of their length and nearly 100% at the anterior region (Figure 2E).

Functional behaviour: The mouth of *P. acuta* was encircled by two lobes of a single lip which lead into the buccal cavity by a short oral tube. When at rest the lateral lobes were apposed longitudinally along the longitudinal axis sealing the mouth closed with the jaw fully retracted. The resting odontophore was folded along its longitudinal axis into a tight U-shaped groove with edges of the lateral pillars curled under. The radular ribbon covered most of the cartilage laying in its concavity and convex surfaces. At the onset of the rasping cycle the lateral lobes of the lip moved away from each other forming a circular opening to the mouth. The jaw was exposed while the odontophore cartilage was rotated forwards and downwards in the buccal mass and protracted through the mouth towards the substratum. The horizontal edge of the "U" (the central region of the odontophore), also referred to as the "tip", made the initial contact with the substratum and as the odontophore continued its rotation the pillars of the "U" were extended outwards and downwards forming a semi-circular fan-shaped disc (Figure 3A). At the same time the radular ribbon moved over the advancing edge of the cartilage. In this inverted position the anterior surface of the radular teeth faced the central row

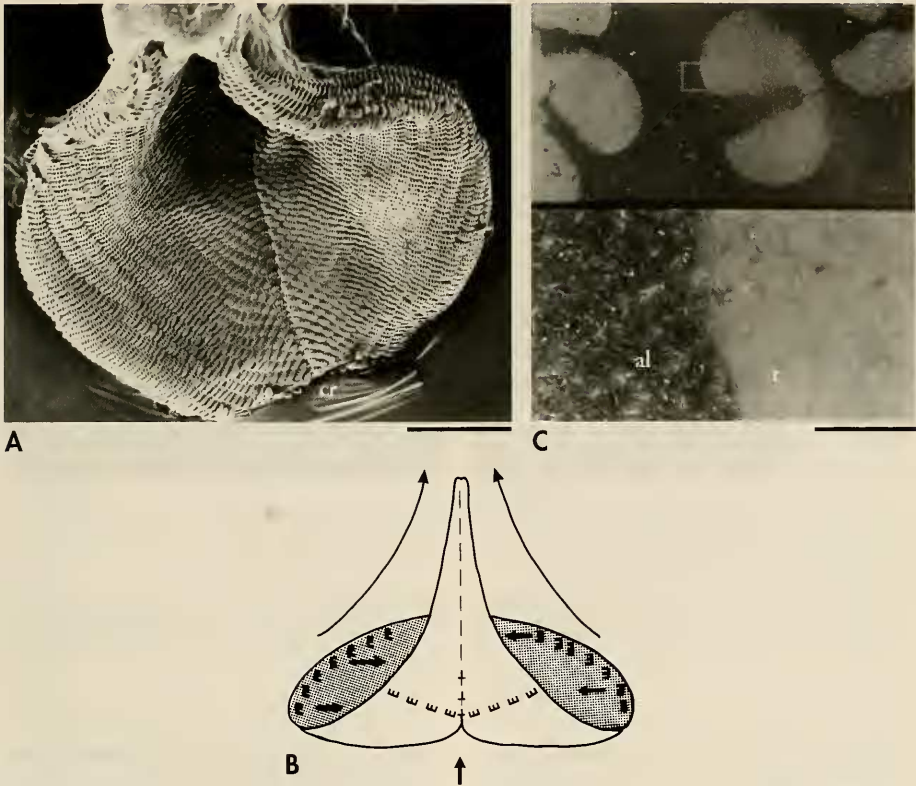


Figure 3. *Physa acuta* SEM. A: radula *in situ* resting on the "U" shaped odontophore with the wings extended; the row of central teeth forms the "dividing line" of the ribbon; B: schematic diagram of radula movement during a rasping stroke; the "E"s represent teeth with projecting cusps; the broken dividing line demarcates the position of the central teeth; C: the resultant radular tracer pattern left behind by the wings of odontophore/ribbon complex; the magnification of the trace clearly shows the efficiency of the radula at removing algae from the substratum. Scale bars, A: 10 μ m, C: 0.5 μ m.

Abbreviations as in Figure 1.

Figura 3. *Physa acuta* MEB. A: rádula *in situ*, sobre el odontóforo en forma de "U" con las alas extendidas; la fila de dientes centrales hace de línea media de la rádula; B: esquema del movimiento radular durante la maniobra de raspado; las "E" representan dientes con sus cúspides; la línea quebrada indica la posición de los dientes centrales; C: patrón de marcas dejado por las alas del complejo rádula/odontóforo; la ampliación muestra claramente la eficiencia de la rádula para levantar las algas del sustrato. Scale bars, A: 10 μ m, C: 0.5 μ m.

Abreviaturas como en la Figura 1.

of teeth. The pillars of the cartilage were then drawn together resulting in the anterior face of the marginals being directed through the algae (Figure 3B). Towards the end of the rasping stroke the odontophore was lifted up from the

substratum and rotated back into the mouth. The jaw was not thought to play a significant role in the feeding cycle.

Unlike *P. acuta*, the lip lobes of *B. tropicus* were prominent, separating asymmetrically with the emergence of the

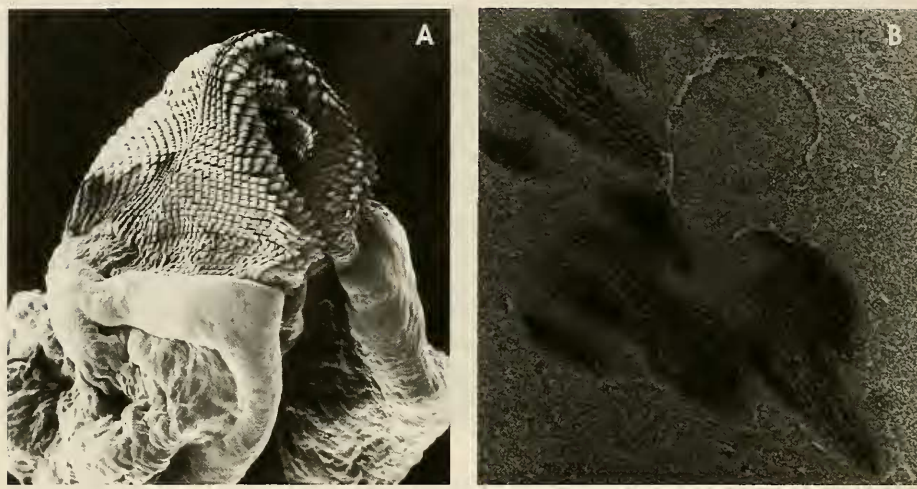


Figure 4. *Bulinus tropicus* SEM. A: radula *in situ* resting on the odontophore; B: radular tracer pattern showing the incomplete removal of unicellular algae from the substratum. Scale bars, A: 100 μ m; B: 260 μ m.

Figura 4. *Bulinus tropicus* MEB. A: rádula *in situ* colocada sobre el odontóforo; B: marcas que deja la rádula, mostrando una eliminación incompleta de las algas del sustrato. Escalas, A: 100 μ m; B: 260 μ m.

wide, scoop-shaped odontophore followed by the projection of the jaw (Figure 4A). The application of the odontophore and radula of *B. tropicus* has been described in detail by STIGLINGH AND VAN EEDEN (1970). Compared to *P. acuta*, the radula of *B. tropicus* appeared fixed to the odontophore such that the long rasping action was directed forwards and control solely by the odontophore and worked against the jaw's cutting edge.

Feeding observations: The feeding trail patterns of *P. acuta* and *B. tropicus* varied from occasional, isolated rasps to a continuum zig-zag. The individual rasps of *P. acuta* involved the use of the whole radula and consisted of two semi-circles hinge posteriorly denoting the "tip" of odontophore and the position of the central teeth which do not appear to be functionally important in gathering food (Figure 3C). The radula was effective at removing most of the algae from the substrate. The rasp patterns of *B. tropicus* were similar to those already described by STIGLINGH AND VAN EEDEN (1970)

and will therefore not be repeated in this paper (Figure 4C). In *B. tropicus* the burden of the rasping action was borne by the centrals and inner marginals.

The efficiency of the radulae to collect different sized food particles varied markedly between the two species (Table I). *Physa acuta* was able to amass all particles sizes ranging from 0.5 μ m (Figure 5) to 12 μ m, but the radula was less efficient when dealing with the filamentous algae. On the other hand the radula of *B. tropicus* was unable to harvest the microspheres and was inefficient at collecting small unicellular algae (Table I) as observed by STIGLINGH AND VAN EEDEN (1970); it only appeared to be effective when rasping filamentous algae in this study.

DISCUSSION

Freshwater rivers in Africa are dynamic systems that can be dramatically altered by floods and/or droughts. This severely impacts on the aquatic

Table I. Average densities of microspheres and algae before and after the feeding action of *Physa acuta* and *Bulinus tropicus*.Tabla I. Densidades medias de microesferas y algas antes y depues de la depredación de *Physa acuta* y *Bulinus tropicus*.

Organism	<i>Physa acuta</i>			<i>Bulinus tropicus</i>		
	Density before	Density after	Efficiency of removal (%)	Density before	Density after	Efficiency of removal (%)
Microspore (0.5 µm)	750/500 µm ²	17/500 µm ²	97.7	750/500 µm ²	739/500 µm ²	1.5
Selenostrum capricorn (6-7 µm)	360/500 µm ²	2/500 µm ²	99.4	360/500 µm ²	301/500 µm ²	16.3
Bumilloeriopsis sp. (10-12 µm)	340/500 µm ²	25/500 µm ²	92.6	340/500 µm ²	199/500 µm ²	58.5
Scenedesmus sp. (18-20 µm)	143/500 µm ²	71/500 µm ²	49.6	143/500 µm ²	9/500 µm ²	93.7

vegetation and the associated fauna. In 1987 and 1988 the Umsindusi River system was profoundly disturbed by flooding on four separate occasions. The invasive snail, *P. acuta*, was able to re-establish itself in significant numbers within one to three months in the absence of aquatic vegetation (BRACKENBURY, 1989). This was possibly due, in part, to a number of characteristics possessed by *P. acuta* viz. high intrinsic rate of natural increase and water current velocity tolerance, year-round breeding, and the lack of predation and parasitism. *Bulinus tropicus* reappeared at a low density nine months or more after the initial flooding. This coincided with the return of aquatic vegetation. A similar pattern was found with *Bulinus truncatus* in Morocco (KHALLAAYOUNE, LAAMRANI AND MADSEN, 1998; KHALLAAYOUNE, MADSEN AND LAAMRANI, 1998). The study by BRACKENBURY (1989) suggested that aquatic vegetation played a significant role in the growth of Aufwuchs as well as providing a source of decaying vegetation. The diet of *P. acuta* and *B. tropicus* in the Umsindusi prior to the floods is unknown, but many studies have shown that freshwater pulmonates such as lymnaeids, physids and planorbids feed on epiphytic and filamentous algae, diatoms, blue-green algae, detritus and decaying vegetation (e. g. STIGLINGH AND VAN EEDEN, 1970; RUNHAM, 1975; MADSEN, 1992; ESTEBE-

NET, 1995). A few species have been found to be selective for filamentous algae e. g. *Lymnaea peregra*, or diatoms e. g. *Planorbis vortex* (LODGE, 1986), but overall pulmonates are non-selective omnivores and the food dimensions are only restricted by the structure of the radula (STIGLINGH AND VAN EEDEN, 1970; HUNTER, 1980; MADSEN, 1992). BRACKENBURY (1989) observed that *P. acuta* utilised the rich supply of diatoms in the denuded habitat of the Umsindusi River, however, *B. tropicus*, remained absent even from quiescent pools of the river regardless of the fact that diatoms were a supposed favoured food (STIGLINGH AND VAN EEDEN, 1970).

The rasping action of *P. acuta* can be described as a combing or mopping movement (STIGLINGH AND VAN EEDEN, 1970) with the radula and odontophore work concurrently, but independently of each other. SMITH (1988) has called this mechanism the "moving-conveyor belt-rasp". At the beginning of the rasping stroke the odontophore cartilage carries the radula towards the substrate and deforms to increase the exposed surface area of the radula. At the same time the radular ribbon moves over the cartilage. During the rasping action the radula and odontophore gradually return to their original positions. As a consequence of this movement consecutive rows of teeth are continually rasped through areas missed by preceding rows during a sin-



Figure 5. *Physa acuta* SEM, high magnification of the lateral teeth (similar to those in Figure 1E) showing the accumulation of the microspheres (mi) (diameter 0.5 μm) on the underside of the crown and cusps as a result of the radula combing the surface of the substratum. Scale bar 2 μm .

Figura 5. *Physa acuta* MEB, ampliación de un diente lateral (similar a los de la Figura 1E) mostrando la acumulación de microesferas (mi) (diámetro 0.5 μm) debajo de la corona y las cúspides, como consecuencia de la curvatura de la rádula sobre el sustrato. Escala 2 μm .

gle feeding cycle. The slight wearing of the cusps supported the supposition that the teeth of *P. acuta* lightly comb or mop the substratum. This feeding strategy plus the high density of teeth, would account for the efficiency of collecting unicellular organisms or fine detritus (0.5 μm to 10 μm). Subsequently, *P. acuta* was capable of effectively exploiting the diatoms and detritus on the substratum of the Umsindusi River, thereby contributing to the species ability to establish itself in a denuded habitat.

The radula and odontophore of *B. tropicus* on the other hand had a different functional relationship which SMITH (1988) described as the iodontophoral lick. In this instance the radula is fixed to the odontophore, and thereby its rasping action is directed and controlled by the underlying cartilage which moves post-anteriorly through the substratum. Consequently, only a single transverse row of teeth at the edge of the odontophore rasps the substratum for the length of the odontophoral stroke. The severe wearing of the cusps is indicative that the radula is applied to the substratum with considerable force to break the algae's attachment to the

substratum. With the use of only one row of teeth any additional food material remaining on the substratum would not be collected. The efficiency is further reduced by the lower density of teeth per unit area in *B. tropicus*. Therefore, the odontophoral lick is considered a relatively inefficient mechanism (SMITH, 1988) resulting in the incomplete removal of small algae (STIGLINGH AND VAN EEDEN, 1970). The radula of *B. tropicus* considered more apt for dealing with filamentous algae and bulk foods as it possesses sharp, robust, cutting laterals (STIGLINGH AND VAN EEDEN 1970) and a jaw which works against the radula resulting in a additional cutting action. Large unicellular organisms would be gathered mostly by the marginals. Consequently, *B. tropicus* was considered to have been ill-equipped to harvest the available food resources in the denuded Umsindusi River habitat and hence its dependent association with marginal and aquatic vegetation.

The present study showed that the radula structure and feeding mechanism of the invasive species, *P. acuta* was markedly different from those of the indigenous species, *B. tropicus*. The

radular structure of each species appeared to determine the range of food resources that they could utilize, which in turn partially impacted on their ability to recolonize the denuded habitat of the Umsindusi River.

BIBLIOGRAPHY

- BRACKENBURY, T. D., 1989. *Some aspects of the biology of Physa acuta (Gastropoda: Physidae) pertinent to its success as an invader in South African rivers*. M. Sc. Thesis, University of Natal, Pietermaritzburg.
- BRACKENBURY, T. D. AND APPLETON, C. C., 1991. Effect of controlled temperature on gametogenesis in *Physa acuta* (Physidae) and *Bulinus tropicus* (Planorbidae). *Journal of Molluscan Studies*, 57: 461-469.
- BRACKENBURY, T. D. AND APPLETON, C. C., 1993. Recolonization of the Umsindusi River, Natal, South Africa, by the invasive gastropod, *Physa acuta* (Basommatophora, Physidae). *Journal of Medical and Applied Malacology*, 5: 39-44.
- BROWN, D. S., 1980. *Freshwater snails of Africa and their medical importance*. Taylor and Francis, London.
- BROWN, D. S., 1994. FRESHWATER SNAILS OF AFRICA AND THEIR MEDICAL IMPORTANCE. Taylor and Francis, London.
- DE KOCK, K. N., JOUBERT, P. H. AND PRETORIUS, S. J., 1989. Geographic distribution and habitat preference of the invader freshwater snails species *Lymnaea colmella* (Mollusca: Gastropoda) in South Africa. *Onderstepoort Journal of Veterinary Research*, 56: 271-275.
- CALOW, P., 1970. Studies on the natural diet of *Lymnaea peregere obtusa* (Kobelt) and its possible implications. *Proceedings of the Malacological Society of London*, 39: 203-215.
- ESTEBENET, A. L., 1995. Food and Feeding in *Pomacea canaliculata* (Gastropoda: Ampullariidae). *The Veliger*, 38: 277-283.
- HAMILTON-ATTWELL, V. L., DE KOCK, K. N. AND VAN EEDEN, J. A., 1970. The occurrence and distribution of *Physa acuta* Draparnaud in the Republic of South Africa. *Wetenskaplike Bydraes van die Potchefstroomse Universiteit vir C. E. O.*, B26: 1-11.
- HUNTER, R. D., 1980. Effects of grazing on the quantity and quality of Freshwater Aufwuchs. *Hydrobiologia*, 69: 251-259.
- KHALLAAYOUNE, K., LAAMRANI, H. AND MADSEN, H., 1998. Distribution of *Bulinus truncatus*, the intermediate host of *Schistosoma haematobium*, in an irrigation system in Morocco. *Journal of Freshwater Ecology*, 13: 129-133.
- KHALLAAYOUNE, K., MADSEN, H., AND LAAMRANI, K., 1998. Evaluation of three methods to control *Bulinus truncatus*, the intermediate host of *Schistosoma haematobium*, in an irrigation system, Tessaout-Amont, Morocco. *Acta Tropica*, 69: 51-63.
- LODGE, D. M., 1986. Selective grazing on periphyton: a determinant of freshwater gastropod microdistributions. *Freshwater Biology*, 16: 831-841.
- MADSEN, H., 1992. Food selection by freshwater snails in the Gezira irrigation canals, Sudan. *Hydrobiologia*, 228: 203-217.
- PIMENTAL, D. AND WHITE JR, P. C., 1959. Biological environment and habits of *Australorbis glabratus*. *Ecology*, 40: 541-550.
- RUNHAM, N. W., 1975. Alimentary canal. In: Fretter, V. and Peake, J. F. (Eds). *Pulmonates* Volume 1. Academic Press, New York.
- SMITH, D. A., 1988. Radula kinetics during grazing in *Helisoma trivolvis* (Gastropoda: Pulmonata). *Journal of Experimental Biology*, 136: 89-102.
- STIGLING, I., VAN EEDEN, J. A. AND RYKE, P. A., 1962. Contribution to the morphology of *Bulinus tropicus*. *Malacologia*, 1: 73-114.
- STIGLING, I. AND VAN EEDEN, J. A., 1970. Notes on the feeding behaviour of *Bulinus (Bulinus) tropicus*. *Wetenskaplike Bydraes van die Potchefstroomse Universiteit*, B, 22: 1-14.
- STIGLING, I., AND VAN EEDEN, J. A., 1976. On the alimentary system of *Bulinus tropicus* with a note on the asymmetrical arrangement of the buccal retractors. *Wetenskaplike Bydraes van die Potchefstroomse Universiteit*, B, 85: 1-28.
- THOMAS, J. D., 1987. An evaluation of the interactions between freshwater pulmonate snail hosts of human schistosomiasis and macrophytes. *Philosophical Transactions of the Royal Society of London*, B, 315: 75-125.
- WILKEN, G. B. AND APPLETON, C. C., 1991. Avoidance responses of some indigenous and exotic freshwater pulmonate snails to leech predation in South Africa. *South African Journal of Zoology*, 26: 6-10.

ACKNOWLEDGEMENTS

The author wishes to acknowledge the assistance of Dr Fiona Graham and Prof. C. C. Appleton, University of Natal, Durban.